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## Embracing in a female-bonded monkey species (*Theropithecus gelada*)

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(Article begins on next page)

1   **EMBRACING IN A FEMALE BONDED MONKEY SPECIES (*THEROPITHECUS GELADA*)**

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17   Key words: geladas, female closeness, embracing variability, grooming

18    **ABSTRACT**

19    In several primate species, including humans, embracing predicts the level of affiliation between  
20    subjects. To explore the functional meaning of embracing we selected *Theropithecus gelada* as a  
21    model species. The basic level of gelada society is the one-male unit and the integrity of the group  
22    is maintained by the strong bonds between females. In our study group, we observed three different  
23    kinds of embracing: the Frontal and Side Embraces involving a face-to-face and chest-to-chest  
24    interaction and the Posterior Embrace which consists in putting the arms around conspecifics' back  
25    and posing a cheek on it. We verified whether the quality of relationships between subjects predicts  
26    the type of embracing. Frontal and Side Embraces were more frequent between females sharing  
27    strong bonds. Posterior Embracing was randomly distributed. We found a high level of female  
28    embracing among the mothers during the first months of lactation. This may improve female  
29    cohesiveness against males thus limiting the risk of infanticide, particularly high in geladas.  
30    Embracing seems also to act as an ice-breaker favoring grooming. In conclusion, female embracing  
31    could be an affiliative strategy which has evolved to maintain group integrity and high social  
32    cohesion among females, especially mothers, who mostly need it.

33  
34    Keywords: geladas; female closeness; embracing variability; grooming

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37           Embracing is a behavior that produces positive physical and emotional experiences (Boeving,  
38   Belnap & Nelson, 2017; Clay & de Waal, 2013; de Waal, 1996, 2000; Forsell & Åström, 2012). In  
39   children and apes, embracing is used to provide comfort to others (de Waal, 2012) and it has been  
40   proposed that it may communicate sympathetic concern (de Waal, 2008; Fujisawa, Kutsukake &  
41   Hasegawa, 2006). In some non-human primate species, embracing behavior may be part of greeting  
42   rituals and functions as a tension-reduction mechanism. Embracing is reported in greeting  
43   ceremonies (black-and-white colobus, *Colobus guereza*, Kutsukake et al., 2006; hamadryas, *Papio*  
44   *hamadryas*, Colmenares, 1991; spider monkeys, *Ateles geoffroyi*, Schaffner & Aureli, 2005; Guinea  
45   baboons, *Papio papio*, Whitham & Maestriperi, 2003) and increases after a period of separation in  
46   species living in fission-fusion societies (spider monkeys, Schaffner & Aureli, 2005; chimpanzees,  
47   *Pan troglodytes verus*, Okamoto, Agetsuma, & Kojima, 2001). These particular societies are  
48   characterized by temporal separations and subsequent re-unions of the subjects of the same group  
49   (Symington, 1987). The spreading of embracing after fusion events has a role in reducing the risk of  
50   aggression (spider monkeys, Aureli & Schaffner, 2007; Schaffner & Aureli, 2005). In short, it  
51   seems to be involved in the management of risky and uncertain encounters (spider monkeys,  
52   Rebecchini, Schaffner & Aureli, 2011; Guinea baboons, Whitham & Maestriperi, 2003; capuchin  
53   monkeys, *Cebus apella*, Lynch Alfaro, 2008). Embracing also plays a role in reducing tension  
54   around preferred resources. Spider monkeys frequently embrace each other to co-feed peacefully  
55   (Pastor-Nieto, 2001). In the same species, when females have young infants, embraces are used by  
56   other females to gain access to infants and manipulate them (Schaffner & Aureli, 2005; Slater,  
57   Schaffner & Aureli, 2007).

58           Embracing does not only have immediate consequences to gain preferred resources but it can  
59   reflect and/or potentiate social bonding between individuals in the long-term. Tonkean macaques  
60   (*Macaca tonkeana*) use clasping (*sensu* Thierry, 1984; including grasping, embracing, hugging and  
61   reaching around) in various contexts to appease (immediate consequence), re-establish and maintain

62 good relationships after conflicts (long-term function) (Thierry, 1984). In muriquis, (*Brachyteles*  
63 *arachnoides hypoxanthus*) male-male hugging is a specific reproductive strategy adopted before the  
64 mating period, presumably to reduce tension over limited resources (the females) during the mating  
65 period (Strier, Dib & Figueira, 2002). Moreover, muriqui males engage in embracing to maintain  
66 peaceful long-term relationships (Strier, Carvalho & Bejar, 2000).

67 *Theropithecus gelada* is a good primate model to investigate embracing, since this behavior is  
68 frequent and highly variable in its expression (Figure 1). Geladas are characterized by male  
69 dispersal and female philopatry (Kawai, Dunbar & Ohsawa, 1983; le Roux, Beehner & Bergman,  
70 2011). They live in a multi-level society in which the basic social group is a one-male reproductive  
71 unit (OMU) including an alpha male, several reproductive females, sub-adult males and females,  
72 infants and juveniles (Snyder-Mackler, Beehner & Bergman, 2012). Both the alpha male and  
73 females are responsible for managing social interactions and maintaining the unity of the group  
74 (Pallante, Stanyon & Palagi, 2016; Palagi, Leone, Demuru & Ferrari, 2018). The alpha male  
75 engages in a high level of affiliation with all group members, even though he does not reach the  
76 level shown by females (Bramblett, 1970; Mori, Belay & Iwamoto, 2003; Mancini & Palagi, 2009;  
77 Palagi, Leone, Mancini, & Ferrari, 2009; Dunbar, 2014). In fact, group stability depends on the  
78 strong bonds shared among females, which form the core of the social unit. Their bonds rely on  
79 mutual grooming, playing, supporting each other during conflicts and providing reciprocal infant  
80 care (Dunbar, 1983, 2014; Dunbar & Dunbar, 1975; Bernstein, 1975; Mancini & Palagi, 2009;  
81 Pallante et al., 2016). Female affiliation is also revealed by the presence of yawn contagion and  
82 rapid facial mimicry, two phenomena of neural-motor resonance that is an index of the emotional  
83 proximity between subjects independently from their genetic relatedness (Mancini & Palagi, 2009;  
84 Palagi et al., 2009). Gelada females have a linear, maternally inherited dominance hierarchy, whose  
85 steepness is weak if compared to other baboon species (le Roux et al., 2011). Due to the peculiar

86 affiliation pattern shown by gelada females, we expect that embracing should be more common  
87 between females than between males and females.

88 In primates, different kinds of embraces can communicate different levels of bonding between  
89 subjects (Lynch Alfaro, 2008; Strier et al., 2002; Whitham & Maestriperi, 2003). Notably, non-  
90 human primates embrace both frontally (symmetric; both individuals display a reciprocal embrace  
91 while engaging in a face-to-face interaction, Frontal Embracing (FE) and Side Embracing (SE) Fig.  
92 1a and 1b) and at the back (asymmetric; one individual embraces the other from the back, Posterior  
93 Embrace, PE; Fig. 1c). For example, in olive baboons (*Papio cynocephalus anubis*, Smuts &  
94 Watanabe, 1990) and in hamadryas (*Papio hamadryas*, Colmenares, Hofer & East, 2000) the  
95 subordinate subject presents the posterior to the dominant, which responds with an embrace at the  
96 back. Therefore, the occurrence of asymmetric embrace (Posterior Embrace) seems to be predictive  
97 of the relative ranking position of the two interacting individuals. If in geladas the Posterior  
98 Embrace has the same function as the one recorded in the genus *Papio*, we expect the distribution of  
99 the Posterior Embrace to be affected by the ranking position of the two subjects, with the higher  
100 ranking individual embracing the posterior of the subordinate. A study on lateralization of face-to-  
101 face embracing (left cheek vs right cheek) in *Ateles fusciceps rufiventris* has recently demonstrated  
102 that this behavior is modulated by emotional states (Boeving et al., 2017). In humans, during an  
103 embrace between strangers and acquaintances the number of body areas contacted is moderate,  
104 while it is higher among friends and between lovers (McDaniel & Anderson, 1998). If in geladas,  
105 the reciprocal embracing involving a face-to-face interaction and a large body part (Frontal and Side  
106 Embrace; Figure 1a and 1b; Supplementary Video S1 and S2) is predictive of the social closeness  
107 between the subjects, rather than by the ranking status, we expect that the phenomenon is affected  
108 by the relationship quality of the individuals involved.

109 In addition to be a behavioral index of the relationship quality among individuals, embracing  
110 might also further sustain bonds under circumstances in which the environment is perceived as

111 dangerous for the individuals, thus requiring group cohesion and coordinated responses. For  
112 example, for a female a highly vulnerable period coincides with the delivery of newborns because  
113 of the risk of infanticide perpetrated by males or predation (wild geladas, Beehner & Bergman,  
114 2008; captive geladas, Pallante et al., 2016; *Papio ursinus*, Palombit, Cheney, Fischer, Johnson,  
115 Rendal et al., 2000; *Papio hamadryas* Henzi & Barrett, 2003). Barrett, Halliday & Henzi (2006)  
116 demonstrated that to cope with the costs of motherhood, female baboons (*Papio hamadryas*  
117 *ursinus*) increased their vigilance levels during the lactation period (the first 4 months after the  
118 delivery). In different species of baboons (*Papio* spp.) living in multi-male/multi-female societies,  
119 male-female “friendship” can act as a deterrent for infanticide to occur (Palombit, Seyfarth, &  
120 Cheney, 1997; Smuts, 1985). In geladas, living in one male units, females can form alliances with  
121 other females against the alpha male (Dunbar & Dunbar, 1975). Females coalitions have a strong  
122 adaptive value, since infanticide perpetrated by alpha males is not rare in geladas and in our study  
123 colony (Pallante et al., 2016). Therefore, during the first months of maternal phase in geladas, the  
124 mothers can gain advantage from seeking social support and cohesion from other adult females. If  
125 this hypothesis is correct, we expect that when a female has a black infant, which is a newborn aged  
126 less than 4 months (lactating period), she would be more prone to initiate/accept embracing  
127 towards/by other females.

128 In the current study we will also assess the potential functional role of embraces in relation to  
129 gain access to other females’ infants, a phenomenon widely described in the genus *Papio* (Frank &  
130 Silk, 2009; Henzi & Barrett, 2002; Silk, Rendall, Cheney & Seyfarth, 2003). In *Papio cynocephalus*  
131 *ursinus*, infant handling is a behavior responding to the biological market rules and it can be  
132 exchanged for grooming (Henzi & Barrett, 2002). Even though females without infants provide  
133 high levels of grooming to mothers in order to gain access to their infants (Henzi & Barrett, 2002),  
134 mothers are attracted by other mothers’ infants and try to handle them at relatively high rates.  
135 Embracing seems also a phenomenon responding to the biological market rules and is performed to

136 increase the probability of accessing to infant, as it has already reported for spider monkeys  
137 (Schaffner & Aureli, 2005; Slater et al., 2007). If embracing is a behavior performed by gelada  
138 females to increase the probability to gain access to other females' infants, we expect that the  
139 lactating mothers (black infant < 4 months) receive more embracing than non-mothers (offspring >  
140 14 months).

141 In primates, behaviors such as grooming, may act as a means to strengthen relationships  
142 among group members. Grooming has been shown to reflect positive dyadic interactions and often  
143 acts as social glue within many primate societies (Dunbar, Barrett, & Lycett, 2005; Schino, Scucchi,  
144 Maestripieri, & Turillazzi, 1988). For example, in black and white colobus embracing has been  
145 reported to strengthen social affiliation by increasing the probability for grooming to occur  
146 (Kutsukake et al., 2006). If also in geladas embracing favors grooming, we expect that an embrace,  
147 more than the mere approach between two subjects, would increase the probability to engage in a  
148 grooming session.

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## Methods

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### Ethics Statement

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Since the study was purely observational, without manipulation of animals, the ethical  
committee of the University of Pisa and Parma waived the need for a permit.

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### Subjects and Data Collection

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We observed two colonies for a total of 40 geladas housed at the NaturZoo (Rheine,  
Germany). The groups were composed of two one-male units (OMUs). For each subject, the exact  
date of birth was known. We identified animals through sex, age and distinctive external features  
such as scars, size, pattern of fur patches, fur color and facial traits. For the age definition and



160 categorization (Table 1) we followed Dunbar & Dunbar (1975). Adult females were 9 in OMU 1  
161 and 7 in OMU 2 (Table 1). All maternal kin relationships were known (Table 1).

162 The two OMUs were set in two different enclosures. Each of the enclosures included an  
163 indoor (about 36 m<sup>2</sup>) and an outdoor facility (2700 m<sup>2</sup> surrounded by a boundary ditch). The  
164 monkeys had continuous access to the indoor and outdoor areas of their enclosures. The outside  
165 enclosures were located in an open, naturally hilly area equipped with trees, where environmental  
166 enrichments like branches, ropes and dens were provided. The food (grass, vegetables and pellets)  
167 was distributed twice a day (9:30 a.m., 2:30 p.m.). Water was available *ad libitum*. No stereotypic  
168 or aberrant behaviors have ever been observed in this group.

169 Before starting the data collection, the four observers underwent a training period of about 30  
170 h. The training ended when the Cohen's kappa was always higher than 0.70 for each behavioral  
171 pattern considered for the study. We checked for observation reliability at the beginning of each  
172 month obtaining values always above 0.70.

173 Animals were observed for 2 three-months periods: in 2010 (June-August) and in 2011 (June-  
174 August). Observations were carried out by four observers with the aid of voice recorders and video  
175 cameras. Grooming was recorded via focal animal sampling.

176 Focal subjects were observed for 30 min each observation day. We focused on one OMU per  
177 day. Therefore, all the subjects of a single OMU were observed at least ones per day (see Table 1  
178 for details on the observed subjects). The observations were balanced across the 6hrs observation  
179 period in order to be sure not to follow the same animal at the same time of the day in consecutive  
180 days. Moreover, the 6 hrs observations were equally spread between morning and afternoon. If the  
181 same embrace was recorded by two different observers who were following two distinct animals  
182 that embrace each other, the behavior was recorded by both the observers but it was counted as a  
183 single event in the analysis.

184 All occurrences sampling technique (2010: 301.5 hours; 2011: 267.4 hours) was used to  
185 collect data on embracing (based on video recordings). We observed three different types of  
186 embracing (Figure 1).

187 Animals spontaneously formed subgroups ranging from 3 to 7 subjects. One observer  
188 continuously video-recorded all the activity of the subjects forming a single subgroup. Before  
189 starting the video analysis, we checked for observation reliability each 3 hs-time block of recording  
190 obtaining values always above 0.75.

191 To build the dominance matrix, all agonistic interactions (chase-fleeing, aggressive  
192 pulling/pushing, slapping, biting) were collected by sampling all occurrences. We recorded the  
193 opponents' identity for each agonistic encounter. The outcome of decided conflicts (with clear  
194 winners and losers) was used to calculate dominance scores.

195 We divided the adult females according to the lactating phase. Female who were lactating  
196 their infants (black infants; <4 months) were clustered as "lactating mothers" (Barrett et al., 2006;  
197 Dunbar, Hannah-Stewart & Dunbar, 2002). In the first 4 months of life, black infants depend almost  
198 exclusively on mothers for food. Females who had yearlings/juveniles aged > 4 months were  
199 clustered as "nonlactating mothers" (Dunbar & Dunbar, 1975).

200

## 201 **Operational Definitions and Statistical Analysis**

202 The observations carried out in 2010 and 2011 permitted us to analyze the influence of the  
203 presence of black infants on mothers' behavior. We compared the hourly frequency of embracing  
204 events initiated by the same mother in two different situations (lactating vs nonlactating) (all  
205 occurrences sampling based on video data collection). Due to the non-normal distribution of data,  
206 we used Wilcoxon test to compare the two conditions.

207 Social bonding was determined dividing the number of grooming sessions (>10 sec)  
208 performed by an actor X toward a receiver Y by the total number of grooming session performed by  
209 X toward everybody (XgrY/XgrALL) (Girard-Buttoz et al., 2014).

210 Kinship was based on maternal lineages (kin coefficient:  $r \geq 0.25$ , paternal sisters excluded)  
211 (Table 1).

212 Hierarchy was assessed by entering decided conflicts involving individuals into a  
213 winner/loser socio-matrix. Rank was measured by Normalized David's Scores. Normalized David's  
214 scores (NDS) were calculated on the basis of a dyadic dominance index ( $D_{ij}$ ) in which the observed  
215 proportion of wins ( $P_{ij}$ ) is corrected for the chance occurrence of the observed outcome. The chance  
216 occurrence of the observed outcome is calculated on the basis of a binomial distribution with each  
217 animal having an equal chance of winning or losing in every dominance encounter (de Vries,  
218 Stevens, & Vervaecke, 2006). The correction is necessary when, as in the case of our study groups,  
219 the interaction numbers greatly differ between dyads. Rank hierarchies were calculated including  
220 only adults. After calculating the Normalized David's Score values (NDS), we expressed as the  
221 NDS difference (deltaNDS) the status rank difference between the actor and the receiver.

222 We ran a General Linear Mixed Models (GLMMs) using the *lme4* package (Bates et al., 2015;  
223 version 1.1.17) in R (R Core Team, 2015; version 3.4.4) to test which variables could affect the  
224 distribution of the different kinds of embracing (face-to-face/chest-to-chest embracing FE+SE;  
225 Posterior Embracing, PE; Figure 1; Table 2). We checked variance inflation factors (VIF) using the  
226 *car* package (Fox & Weisberg, 2011) and found that all VIF were below 2, showing the absence of  
227 collinearity. We ran a first GLMM to test whether the likelihood of embracing FE+SE (Table 2)  
228 was influenced by the difference in rank between the individuals (deltaNDS), by the level of social  
229 bonding within the dyad, and by the mothering status of the partners (mother vs. non-mother). We  
230 built the model using the number of FE + SE events as the response variable, the minutes of  
231 observation as offset (after log-transformation), the rank difference between the partners, the level

232 of social bonding, the mothering status of the partners (0=nonmother-nonmother; 1=nonmother-  
233 mother; 2=mother-nonmother; 3=mother-mother) as fixed factors, the level of kinship between the  
234 partners (0=nonkin;1=kin) as a control predictor, and identity of the actor, identity of the partner,  
235 and the year of observation as random factors. We verified the assumptions that the residuals were  
236 normally distributed and homogeneous by looking at a qqplot and the distribution of the residuals  
237 plotted against the fitted values (using a function written by R. Mundry). Once excluded the  
238 collinearity between predictors (see Estienne et al. 2017), we tested the significance of the full  
239 model (Forstmeier & Schielzeth, 2011) by comparing it against a null model comprising the control  
240 predictor and the random factors only, by using a likelihood ratio test (Anova with argument test  
241 “Chisq”; Dobson, 2002). We calculated the P values for the individual predictors based on  
242 likelihood ratio tests between the full and the respective null model by using the R-function “drop1”  
243 (Barr et al., 2013; Mundry & Nunn, 2009; Mundry, 2011). Then, we ran a second GLMM with the  
244 same predictors, controls, and random factors, which included the number of PE (Table 2) as the  
245 response variable, to test whether the likelihood of PE was influenced by the same factors.

246 To assess whether the presence of embracing ( $AP_{\text{embracing}}$ ) favored the initiation of a grooming  
247 session compared to a simple approach between the subjects ( $AP_{\text{NO-embracing}}$ ), we ran a binomial  
248 GLMM. We used the presence/absence of grooming as the dependent variable (0 = absent; 1 =  
249 present), presence/absence of embracing after an approach as a predictor (0 = absent; 1 = present),  
250 kinship, bonding, deltaNDS, and mothering status of the partners as control factors. We entered the  
251 identity of the actor, identity of the partner, and the year of observation as random factors (Table 3).  
252 We used the same steps presented above to test the model and derived the significance of the single  
253 predictors.

254

255

## Results

256 Embracing is a phenomenon which involved exclusively adult and subadult females.  
257 Therefore, we focused subsequent analyses on females only. Adult females performed both face-to-  
258 face/chest-to-chest embracing ( $FE + SE_{\text{mean hourly frequency} \pm SE} = 0.0102 \pm 0.00118$ ) and Posterior  
259 Embracing ( $PE_{\text{mean hourly frequency} \pm SE} = 0.0027 \pm 0.00051$ ).

260 In our first model investigating which variables affected the likelihood of embracing  $FE + SE$ ,  
261 the full model was significantly different from the null model. Face-to-face/chest-to-chest embraces  
262 were more frequent between mother-mother dyads and positively influenced by the strength of their  
263 bond (Table 4; Figure 2 and 3). On the other hand, kinship had a negative effect on the number of  
264 embraces, as  $FE + SE$  were more spread among non-kin females (Table 4).

265 In our second model investigating which variables affect the likelihood of embracing  $PE$  the  
266 full model was not significantly different from the null model. When comparing the full versus the  
267 null model using the likelihood ratio test for the  $PE$ , we did not find any significant difference (Full  
268 vs Null:  $\text{Chisq} = 8.644$ ,  $df = 5$ ,  $P = 0.124$ ). Thus, we could not proceed calculating the significance  
269 of the single predictors.

270 Since our study covered two years, we had the possibility to gather data on the same seven  
271 females in two different conditions: when they were lactating (0-4 month black infant) vs when they  
272 were not lactating (the same mother without any black infant). The comparison revealed that when  
273 the females changed their status they concurrently also changed their levels of embracing. When the  
274 females were lactating they engaged in higher levels of face-to-face/chest-to-chest embracing than  
275 when they were not lactating (Wilcoxon's  $T=1.00$ ; ties=0;  $N=7$ ;  $p=0.028$ ).

276 Due to the random distribution found for the Posterior Embracing ( $PE$ ), to test the prediction  
277 about the role of embracing in facilitating grooming interaction, we focused the analysis on the  
278 face-to-face/chest-to-chest embracing ( $FE+SE$ ). We found that the full model including response,  
279 predictor, control factors and random factors significantly differed from the model including

280 response against the random factors (null model). The occurrence of embracing, but not the other  
281 predictors, had a significant effect on the onset of grooming (Table 5).

282

283

## Discussion

284 In the current study, we showed that in geladas embracing is exclusively performed by adult  
285 females who engaged in this behavior more frequently during the first months of lactation (Figure  
286 3). Social bonding did affect the distribution of the different embracing patterns (Figure 1).  
287 Compared to Posterior Embrace, Frontal and Side Embraces, involving face-to-face and chest-to-  
288 chest interactions, were more common between strongly bonded (Figure 2) and non-kin related  
289 females.

290 In humans, different forms of touching can communicate different emotional states  
291 (Hertenstein, Keltner, App, Bulleit, & Jaskolka, 2006). Studying human embracing, McDaniel &  
292 Anderson (1998) found that the number of body areas entering in contact was higher among friends  
293 and lovers. For example, in humans warm touching and embracing often signal an individual's  
294 prosocial motivation and cooperative intent (Frank, 2002; Hertenstein et al., 2006). The different  
295 types of embraces in geladas also seem to convey different meanings. Frontal (face-to-face) and  
296 Side (chest-to-chest) Embraces (Figure 1a and 1b), contrary to Posterior Embracing, were more  
297 frequent between subjects sharing strong social bonds (Figure 2). In contrast, Posterior Embracing  
298 (Figure 1c), the asymmetric form, was randomly distributed. Thus, the type of embrace can predict  
299 the quality of relationships between adult gelada females. In this view, human and gelada  
300 embracing seem to show some interesting common functional features. The similar use of  
301 embracing involving a face-to-face/chest-to-chest interaction between strongly bonded subjects  
302 underlines that for both species this behavior probably plays an important role in maintaining good-  
303 quality of relationship, or friendship.

304 From a functional point of view, embraces in geladas appear to have a similar role to that  
305 observed for grunts in baboons. In female baboons (*Papio cynocephalus ursinus*) grunt  
306 vocalizations signal a benign intent favoring immediate affiliative contacts (Cheney, Seyfarth, &  
307 Silk, 1995). Interestingly, grunts facilitate social interactions especially among unrelated females.  
308 As it occurs for grunts in baboons, in geladas embraces are exchanged more frequently between  
309 non-kin than between kin females. By embracing each other, unrelated females probably reinforce  
310 their cohesion thus coping with potential unpredictable interactions. This is particularly important in  
311 geladas, whose relationships are not based on nepotism but rely on the strength of social bonds.

312 The link between face-to-face embracing and grooming is strengthened by their temporal  
313 association. A grooming session was more likely to occur after an embrace than after a simple  
314 physical approach, independently from the characteristics of the partners. This result is in line with  
315 the hypothesis that behaviors which can be potentially risky (during an embrace animals expose  
316 vulnerable body areas, i.e. head and ventrum) function as 'ice-breakers' and facilitate the  
317 occurrence of grooming (Cheney et al., 1995, Kutsukake et al., 2006).

318 On the contrary, the Posterior Embracing seemed not to be affected by any variables  
319 considered for the analysis, including the NDS values of the subjects. Our result contrast with  
320 previous observations on baboons, where high ranking subjects embrace the back of subordinates  
321 who present the posterior (Colmenares, 2000; Smuts & Watanabe, 1990). The fact that Posterior  
322 Embracing is not affected by rank can be explained by the very shallow hierarchical steepness in  
323 geladas. In this species, hierarchy is fluid and plays a less central role in social dynamics and group  
324 organization compared to baboons, especially among females, whose social bonds represent the  
325 most important glue of the society. However, since Posterior Embracing was observed at very low  
326 frequency, this hypothesis needs further support by additional data collections on other colonies.

327 The higher activity in embracing behavior recorded between gelada mothers during the  
328 lactating phase supports the view that this phenomenon is associated to specific phases of females'

329 life cycle. In mammals, the endocrine changes occurring during the first phase of lactation seem to  
330 be one of the proximate factors influencing females' responsiveness towards their infants  
331 (Maestripieri, 2001). Human and non-human mothers interact emotionally with their newborns  
332 through mutual gaze (Ferrari, Paukner, Jonica & Suomi, 2009; Stern, 1985; Trevarthen, 1974, 1980;  
333 Tronick, 1989) and touch stimulation (Palagi, 2018). This positive affective process can then  
334 encompass different types of social interactions, from the mother-infant one to adult-adult  
335 interactions (either with kin or non-kin individuals), thus expanding such affective exchanges to  
336 other social domains. Our findings on embracing behavior of mothers during lactation support this  
337 view. During the lactation period human and non-human primate mothers produce high levels of  
338 plasma oxytocin, which has been reported to increase the motivation to engage in behaviors  
339 fostering social attachment (Feldman, Weller, Zagoory-Sharon, & Levine, 2007; Levine, Zagoory-  
340 Sharon, Feldman, & Weller, 2007; Light, Grewen & Amico, 2005; Simpson, Sclafani, Paukner,  
341 Hamel, Novak, et al., 2014). This could be one of the proximate mechanisms which sustains the  
342 high frequency of embracing behaviors we assessed between gelada lactating mothers. This  
343 hypothesis clearly requires further investigation as it has also important implications for our  
344 understanding of the mechanisms regulating social behaviors in nonhuman primates.

345       Even though specific analyses on infant handling are not provided here, we cannot exclude a  
346 link between embracing among mothers and infant access. For instance, Silk et al. (2003) observed  
347 that female baboons (*Papio cynocephalus ursinus*) were more attracted by other infants when they  
348 had their own infants. Again, the functional similarity between grunts in baboons and embracing in  
349 geladas appears evident. Females of chacma baboons grunts more frequently to mothers compared  
350 to non-mothers and the use of grunts increases the access to others' infants (Silk, Seyfarth, &  
351 Cheney, 2016). As for grunts, embraces may function as a tension reduction mechanism which  
352 creates the condition for social interaction to occur especially when the interacting subjects share  
353 uncertain relationship (Silk et al., 2016). In this view, we cannot exclude that embracing may play a



354 role in facilitating infants' access and be part of the biological market linked to infant handling also  
355 in such a female-bonded and tolerant species.

356 From a functional perspective embracing may be an adaptive behavior favored by natural  
357 selection; in some primate species females are highly prone to form strong social networks, which  
358 can ensure higher survival and fitness (Furuichi, 2011; McFarland & Majolo, 2013; Seyfarth &  
359 Cheney, 2013). Embracing in geladas is particularly frequent during the first months of lactation,  
360 when females can benefit from others' females support to better protect their infants from potential  
361 infanticidal males. Interestingly, in some species of baboons living in multi-male/multi-female  
362 society, females can reduce infanticide risks by increasing their bonds with males and thus  
363 supporting each other in defending the offspring (Smuts, 1985; Palombit et al., 1997). In wild  
364 savannah baboons, Silk and co-workers (Silk, Alberts & Altmann, 2003) found that females affiliate  
365 with other females to limit the harassment by males and enhance infant survival (Barrett et al.,  
366 2006). Geladas live in a female-bonded society and one of the core factors strongly affecting their  
367 fitness is female strong affiliation and agonistic support also against males (Dunbar, 2014; Pallante  
368 et al., 2016). In our studied colonies we have reported some cases of infanticidal behaviors  
369 perpetrated by males (Pallante et al. 2016) and we observed one infanticide event also during our  
370 data collection. We therefore hypothesize that female affiliation in geladas can be a potential tool to  
371 prevent the infanticide perpetrated by males, a common phenomenon in this species (Beehner &  
372 Bergman, 2008; Mori, et al., 2003; Pallante et al, 2016). This hypothesis is also supported by our  
373 data showing that embracing increased during the first four months of lactation (black infants), a  
374 high-risk period for infanticide. The finding that embraces are more spread among unrelated  
375 females is essential in this sense. During an attack by the alpha males, a female receives more  
376 frequently aid by her kin, given the inclusive fitness benefit that the supporter would gain from her  
377 intervention (Hamilton, 1964). On the other hand, gelada females may exchange embraces with  
378 non-kin in order to strengthen bonds with unrelated subjects and, as a consequence, increase a

379 potential cooperation with them. This mechanism is particularly important to maintain good  
380 relationships among non-kin, given that the benefit provided by the aid of an unrelated subject relies  
381 on reciprocal altruism more than on genetic advantages (Hamilton, 1964). In this perspective, by  
382 increasing their levels of embracing gelada females may strengthen their cohesiveness against  
383 potentially infanticidal males, and thus limiting the risk of losing their offspring.

384 In conclusion, in geladas the different types of embracing can have different meanings. The  
385 embraces characterized by a face-to-face and chest-to-chest interaction are exclusive to adult  
386 females which share strong bonds. The bonding hypothesis clearly requires further investigations in  
387 order to understand whether this females' strategy could be one of the possible mechanisms at the  
388 basis of the maintenance of group cohesion, also in absence of the dominant male.

389

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399

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591

592

## 593 **Figure legends**

594

595 **Figure 1.** The different kinds of gelada embraces. The Frontal Embrace (FE) consists in putting one  
596 or both arms round neck/chest of the other, who responds in the same way (Figure 1a). The Side  
597 Embrace (SE) consists in putting one arm over and one arm under the shoulder of the other

598 individual while rotating the trunks in opposite directions (Figure 1b). Both FE and SE involve a  
599 face-to-face and chest-to-chest interaction between the embracers who show a reciprocal behavior.  
600 The Posterior Embrace (PE) consists in putting the arms around the back/waist of the conspecific  
601 and posing a cheek on it (Figure 1c). This kind of embracing is obviously not reciprocated.

602

603 **Figure 2.** Scatter plot showing the frequency of Frontal and Side Embracing (FE + SE) as a  
604 function of the relationship quality (social bonding) of the dyads involved.

605

606 **Figure 3.** The graph shows the frequency of Frontal and Side Embracing (FE + SE) (mean  $\pm$ SE) as  
607 a function of motherhood condition.

608

609

610 **Video S1** - The video shows two adult females with their black infants. At 00:01, the female on the  
611 left lip-smacks towards the female on the right side. At 00:02 the female on the left side initiates a  
612 Frontal Embracing behavior (FE). At 00:04 the female on the left side stands up and the two  
613 females initiate a face-to-face interaction while embracing each other. One of the black infants is  
614 looking at them. At 00:06 the female who initiated the embracing interaction begins to groom the  
615 female on the right.

616

617 **Video S2** - The video shows two adult females sitting in contact. At 00:01, the female on the left  
618 side initiates a Side Embracing (SE) with the female on the right side. At 00:02, the female on the  
619 right side lip-smacks towards the other female and reciprocate her embrace. At 00:10 the female on  
620 the left side, who had initiated the embrace, begins to groom the other female.

621